THE NORTH COAST BIODIVERSITY ARENA IN CENTRAL CALIFORNIA: A NEW SCENARIO FOR RESEARCH AND TEACHING PROCESSES OF EVOLUTION

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Abstract

The factors responsible for variation in evolutionary rate and pattern among related plant taxa remain in large part obscure. Neutral or selectionist theories alone cannot account for divergent rates of morphological and molecular evolution among related lineages. Interactions among population histories, inherent genetic capacities and environment influence divergence rate. The development of a concise modern evolutionary synthesis, incorporating molecular data and transcending the neo-Darwinian synthesis, is complicated by interaction of these highly complex variables. Control or limitation of these variables is necessary if further evolutionary research is to result in a new synthesis. To this end a biogeographic region is delimited within north-central coastal California and termed the 'North Coast Biodiversity Arena' (NCBDA). The NCBDA has a relatively well-understood geological and environmental history. It is a region of marked microclimatic and edaphic discontinuities, but not one of extreme environments. In general, the climate displays a gradient of decreasing precipitation west to east with simultaneously decreasing equability. It is restricted by definition to elevations below 500 meters. Without high mountain ranges within its boundaries killing frost is essentially unknown. Its topography is varied and in some areas rain shadows have strong local effects. The NCBDA supports a highly diverse flora including both habitat specialists and broadly adapted species. The diversity of major vegetation types, floristic associations, edaphics, and geologies within the NCBDA is introduced. Evolutionary problems critical to the development of a modern evolutionary synthesis and whose solutions may be accessible within the NCBDA are described.

In the mid-1930's, biologists seeking to explain the causes of evolution had reached a point comparable to that which they face at present with respect to the question "Where do we go from here?" Theodosius Dobzhansky provided the stimulus for biologists of different disciplines to combine in constructing the twentieth century (neo-Darwinian) theory by publishing his book, "Genetics and the Origin of Species" (1937). Relevant facts and accessory theories were provided by Julian Huxley in natural history, Sewall Wright and

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Ronald A. Fisher in population genetics, Ernst Mayr in animal systematics, G.G. Simpson in paleontology, Bernhard Rensch in animal phylogeny and macroevolution, and G. Ledyard Stebbins in plant evolution.

This mid 20th century synthetic theory, in which natural selection was a prominent feature, lasted for thirty years until it was challenged by two new approaches, one theoretical and the other based upon new facts and techniques. Calculations by Zuckerkandl and Pauling (1962) led to the concept of regular and constant rates of evolution—the Evolutionary Clock. Such a clock would be independent of Darwinian natural selection. If its action were based upon internal, genetically determined factors, regardless of environmental factors, it would relegate the Darwinian concept of evolution to a minor status. Almost contemporaneously, Kimura (1964, 1968) based on his concept of population dynamics, maintained that at the molecular level mutations are neutral with respect to adaptation and so selection must be of minor importance in evolution. Almost immediately after Kimura's first exposition of his neutral theory, Harris (1966) dealing with humans and Lewontin and Hubby (1966) in populations of *Drosophila,* revealed the presence of enzyme differences between and enzyme polymorphism within populations at gene loci that have no obvious effect on adaptation or fitness. Shortly afterward, Kahler and Allard (1970) found a similar situation in plant populations.

The violent controversy that arose from these attacks on Darwinian natural selection raged for twenty years without a consensus and is just now simmering down. Although differences exist among modern evolutionists, neither the extreme view taken by Kimura and early followers of Zuckerkandl and Pauling, nor the prevailing viewpoint of the mid-twentieth century synthetic theory that minimized the importance of neutral mutations, is currently held by modern synthetic evolutionists. The issue between selection and chance is not plus or minus, but one of degree.

As opposed to the 1930's, during the 1990's zoologists and botanists alike are leading the way to a new synthesis incorporating new discoveries this time based upon processes at the molecular level. The recent review of both facts and theories by John Avise (1993) should be studied by all modern synthetists as carefully as was Dobzhansky's review by their predecessors. Although Avise emphasizes metazoan examples, he does include careful accounts of examples from plants.

Most important, his synthesis reflects the demonstration by Watson and Crick (1953), that point mutations are errors in copying. Hence they can be expected to occur much more often than was believed possible before 1950, when mutations were believed to be reorganizations of complex protein molecules (Schrodinger 1944).

Although Gillespie (1991) has provided stimulating material based upon both theory and calculations suggesting that mutations effecting amino acid sequence substitutions in proteins may not be neutral; high frequencies of neutral mutations, if they do exist, are not incompatible with molecular theory which postulates that adaptively significant mutations occur at frequencies high enough to explain the origin of races and species.

With reference to plant evolution, a line of evidence that has developed during the past thirty years indicates that many modern species of woody angiosperms, which have a better fossil record than herbs, have remained morphologically constant for millions of years (Axelrod 1975, 1979, 1985, 1992). Much evidence supports a general combination of the older idea of slow or static evolution, or bradytely, punctuated with much more rapid evolution, or tachytely (Simpson 1944, 1953). Modern evolutionists have largely supported this concept of episodic evolution, or punctuated equilibria (Eldredge and Gould 1972).

A further development from these new discoveries and theories is that rates of phenotype evolution with respect to diagnostic characters of form may or may not agree with rates of biochemical evolution based directly on mutations. Leslie Gottlieb's research on *Clarkia* has shown that in some evolutionary lineages (e.g., *Clarkia biloba-lingulata*) (Gottlieb 1974) morphological and cytological differences are greater than biochemical differences. In other lineages (e.g., *Clarkia rubicunda-franciscana*; Gottlieb 1973) biochemical differences are accompanied by essentially no change in form. Since information obtained from a single genus is subject to so many difficulties of extrapolation from one genus to another, results obtained before the availability of molecular methods cannot be applied to a new synthesis embodying molecular data unless the groups are reinvestigated using molecular methods. Further complicating the development of a new synthesis is the fact that different kinds of adaptive differences may be controlled by different kinds of gene systems. For instance, Clausen and Hiesey (1958) after analyzing covariation of vegetative and reproductive characters among more than 550 F_2 progeny of artificial hybrids between high elevation races and either foothill or coastal races of *Potentilla glandulosa,* found that individual vegetative differences such as overall size, leaf shape and timing and degree of dormancy, are each governed by a larger number of gene loci than are individual reproductive differences such as petal size and color, and seed size. These discrepancies show that new investigations will lead to a new synthesis only if they are designed and conducted in such a way as to reduce to a minimum the number of variations with which one must deal.

The facts reviewed have brought about a dilemma that must be resolved before a new evolutionary synthesis can be constructed. On the one hand, molecular genetics and developmental physiology favor a clock-like equalization of evolutionary rates. On the other hand, successions of phenotypes through time indicate a highly episodic alternation of rapid and slow rates, the slowest of which amount to evolutionary stasis. In addition, these inequalities of evolutionary rate may affect closely related lineages. Genera with common ancestors such as *Arbutus menziesii* vs. *Arctostaphylos* in the Ericaceae, or *Lithocarpus densiflora* vs. *Quercus* in the Fagaceae display clear differences in rates of differentiation between their respective lineages. On the one hand *Arbutus menziesii* has a fossil record covering 25–30 million years over which little or no morphological change has occurred (Axelrod 1992). On the other hand the closely related and certainly no older genus *Arctostaphylos* has undergone extensive morphological modification resulting in the presence of some 80 more or less well-differentiated forms in California (Wells 1993). Clues to the answer to this question rely upon comparisons between purposeful change produced by animal and plant breeders and the opportunistic changes of which Darwinian evolution consists. Plant and animal breeders have shown that even if directional selection is based upon combinations of mutations each of which by itself has a small effect, they can produce great transformations during periods of time no longer than 100–300 years. Although comparable rates in natural evolution can occur under unusual conditions of strong selection, most evolutionary modifications require tens of thousands or even millions of years. We must conclude that rates of evolutionary change depend not solely upon intrinsic attributes of the organisms themselves, but upon external factors that inhibit or promote the innate capacities of the organisms.

THE VALUE OF SELECTED BIOGEOGRAPHIC REGIONS

Obviously, evolutionists seeking answers to these questions must understand the complexities of the environment with respect to both its present condition and past history just as thoroughly as they must understand the genetic structure and developmental physiology of the organisms that inhabit it. We propose that the most efficient pathway by which a comparable understanding of both organismal and environmental factors within an area may be accomplished is to concentrate upon a natural physiographic and biogeographic region that is so restricted and accessible that it can become well understood. A region so delimited should be one which has a known history of geologic and climatic change during past millions of years, and at the same time contains taxa composed of populations found more or less throughout the region. The region should have general environmental homogeneity except for a limited and comprehensible range of factors. Since any analysis requires alternation between

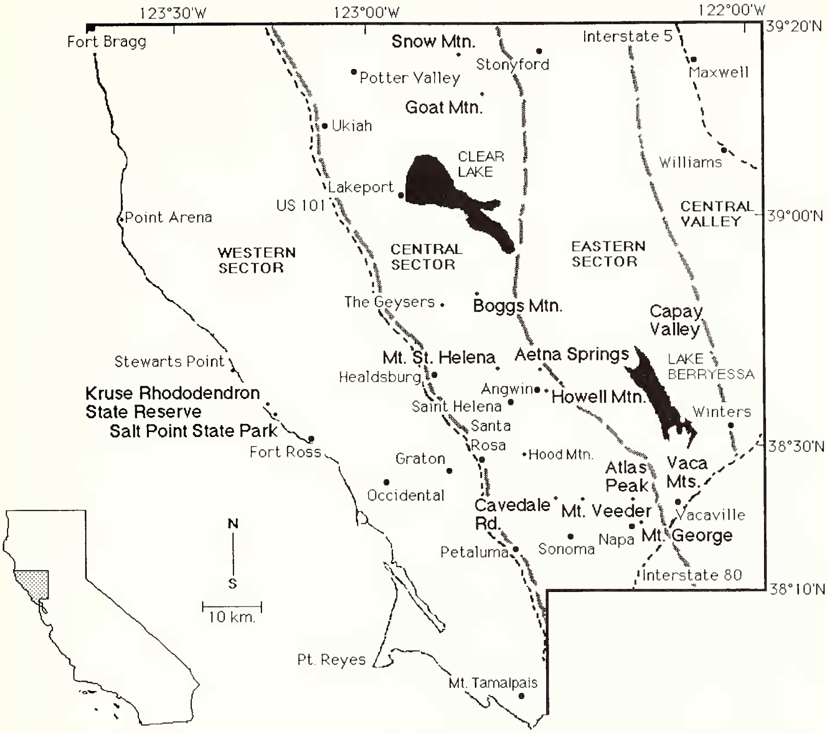

FIG. 1. Map of the North Coast Biodiversity Area in Central California. Geographic features, reserves, parks and cities shown are those discussed in the text, listed in Table 1, or are provided for orientation and clarification.

observations in nature and controlled experiments in the laboratory, the selected region should be easily accessible to well equipped laboratories (see Appendix II).

THE NORTH COAST BIODIVERSITY ARENA

These desirable features are characteristic of the region between 38°10′ and 39°20′ north latitude, extending from the western margin of California's Central Valley, across the North Coast Ranges to the Pacific Ocean (Fig. 1). We propose that this region be designated the North Coast Biodiversity Arena (hereafter referred to as the NCBDA). Because Marin County shares most of the biological and geographical features that make the NCBDA of special interest, it must be included in it as well. Thus, the NCBDA includes all of Marin, Napa, and Sonoma Counties, most of Lake County, the southern portion of Mendocino County and all of western Colusa County. In floristic terminology (Hickman 1993), the NCBDA in-

TABLE 1. MEAN ANNUAL PRECIPITATION AND ANNUAL RANGE OF MEAN TEMPERATURES OF WARMEST AND COLDEST MONTHS AND CALCULATED EQUABILITY *M* (SEE AXELROD 1967 p. 7) FOR SELECTED SITES WITHIN THE NCBDA. Dashes indicate unavailable site data. See Figure 1 and text for sector delimitation and Figure 1 for site location.

Site	NCBDA sector	Annual precipitation (mm)	Range of means/ Equability (*M*)
Fort Bragg	western	1013	5.6°C/*M* 72
Fort Ross	western	1030	5.3°C/*M* 74
Graton	western	1043	11.3°C/*M* 64
Occidental	western	1366	—
Point Arena	western	—	5.4°C/*M* 73
Angwin	central	1028	15.7°C/*M* 59
Healdsburg	central	1074	13.2°C/*M* 59
Lakeport	central	759	17.3°C/*M* 55
Napa	central	630	11.1°C/*M* 64
Petaluma	central	627	11.2°C/*M* 63
Potter Valley	central	1153	15.8°C/*M* 57
Saint Helena	central	899	13.8°C/*M* 61
Santa Rosa	central	780	11.6°C/*M* 63
Sonoma	central	715	12.8°C/*M* 60
Ukiah	central	999	15.4°C/*M* 58
Stonyford	eastern	505	19.3°C/*M* 53
Winters	eastern	524	18.0°C/*M* 53
Lake Berryessa	eastern	—	17.4°C/*M* 53
Vacaville	eastern	649	16.9°C/*M* 55

cludes the southern parts of the Inner and Outer North Coast Range subprovinces (NCoRI, NCoRO), and southern North Coast (NCo) subprovince. The present review will describe the ranges of climatic and edaphic variation within this area, the different plant associations that it supports, preliminary notes on these associations that include *Sequoia sempervirens,* and a discussion of specific taxa which present evolutionary problems appearing particularly suitable for investigation within the NCBDA. Throughout the following discussion nomenclature follows Hickman (1993) except where specifically stated.

The NCBDA is divisible into three longitudinal sectors, as illustrated in Figure 1. Among them, the sectors differ in climate (Table 1) and relative frequency of different plant associations. The eastern sector extends from the NCBDA margin near Vacaville, Winters and Williams to the divide between the Putah Creek drainage and the Napa Valley, extending northward to near Stonyford in Colusa County. This eastern sector is devoid of summer fog and subject to high summer temperatures. Its forest associations are confined to oak woodland (*Quercus wislizenii, Quercus kelloggii*) and savanna

(*Quercus douglasii, Quercus lobata*) with several stands of *Cupressus sargentii* (Sargent cypress) near the western boundary. This sector is the southern part of the Inner North Coast Range (NCoRI) floristic subprovince.

The central sector includes the Napa and Sonoma Valleys, the intervening Hood Mtn.–Mt. Veeder ridge, the Mayacmas Range, and the rugged hilly region north of Clear Lake. The western limit of the central sector lies roughly near US highway 101 (see Fig. 1). Although the central sector peaks and ridges are mostly lower and drier than the Coast Ranges to the north, the rough topography, varied parent materials and diverse soils nevertheless enable this sector to support a highly diverse and discontinuous flora with numerous examples of different plant associations in proximity. Both mean annual precipitation and temperature extremes are intermediate between eastern and western sector values (Table 1). Except for the strictly coastal *Pinus muricata* (bishop pine), all of the tree species occurring in the entire NCBDA are represented in the central sector; only *Pinus ponderosa* (ponderosa pine) and *Calocedrus decurrens* (incense cedar), both highly localized within the NCBDA, are restricted to it. Obviously, the intermediate ecological status and wealth of restricted habitats found within the central sector make it the most likely region to contain interesting examples that shed light upon both the causes of endemism and the ecological factors that affect speciation.

The western sector is dominated by climax redwood forest and the mixed evergreen associations (sensu Munz and Keck 1949, 1950); these merge along the sector's relatively sunny eastern boundary. A strictly coastal association, dominated by *Pinus muricata*, separates the redwood association from the actual coast except within a few sheltered canyons where redwoods approach the ocean margin.

Confined in the NCBDA to the western sector are several herbaceous and shrubby species such as western burningbush *Euonymus occidentalis* (western burningbush), *Scoliopus bigelovii* (slinkpod), *Clintonia andrewsiana* (red clintonia), *Vancouveria planipetala* (inside-out flower), *Hierochloë occidentalis* (sweet grass), and *Vaccinium parvifolium* (red huckleberry), all regarded by California botanists as typical of redwood forests, but equally well known to botanists familiar with Oregon and Washington as growing beneath *Pseudotsuga menziesii* (Douglas fir), *Tsuga heterophylla* (western hemlock) and other conifers.

Principal Climatic Parameters of the NCBDA

I. Temperature (see Table 1). The NCBDA lies entirely at elevations below 500 meters within central California, and so does not include any areas subject to killing frost or snow; frost prone regions within its boundaries but theoretically excluded from the NCBDA include the highlands of Mt. St. Helena, Boggs Mountain, Goat Mountain and Snow Mountain, all within the central sector.

The NCBDA is entirely within the summer-dry Mediterranean climate region, suffering most of the warm season without significant precipitation. Drought stress is greatly alleviated in the western sector where almost daily fog keeps the maximum temperatures down to 19°C (66°F) and maintains atmospheric humidity of 50% or higher during the critical middle parts of the day. The sector is also one of mild temperatures with high equability ($M \pm 70$ see Table 1) and a generally low range between means of the warmest and coldest months of the year (Table 1). Central sector temperatures, humidities and equabilities are intermediate and vary greatly between adjoining localities, depending upon features of the rugged topography and their effects on wind direction, whether oceanic or landward. In this central region, adjacent or nearby plant populations may be exposed to very different temperature and moisture regimes, such that cross fertilizing species dependent upon insects and other vectors often will produce progeny that are highly heterozygous for alleles controlling adaptations to tolerance of temperature and moisture stress.

II. Precipitation (see Table 1). Mean annual precipitation values recorded by weather stations along or adjacent to the North Coast Biodiversity Arena (NCBDA) vary from approximately 500 mm (20 inches) at Winters in the Central Valley, to 1030 mm (41 inches) at Fort Ross on the coast, and 1360 mm (54 inches) at Occidental in the western sector redwood forest. Central sector precipitation values are intermediate and highly variable, depending on the presence or absence of the local rain shadows that abound in the rugged terrain.

Nevertheless, even these great differences fall within the tolerance ranges of an unknown but probably fairly high proportion of the species that occur within the NCBDA, since some of them e.g., *Quercus kelloggii* (California black oak), *Mimulus aurantiacus* (sticky monkeyflower), and *Clarkia concinna* (red ribbons) are almost equally common in both the western and eastern sectors. In many instances, differences in edaphic distribution may compensate for climatic differences, so that a population growing in a relatively low moisture region may possess genotypes adapted to shady localities or relatively heavy soils having high water holding capacity, while other populations of the same species may be adapted to moister climates, but to soils with low water retention. Overall a major problem confronting plant ecologists interested in evolution is the presence, absence, frequency and significance of compensating adaptive equilibria. The North Coast Biodiversity Arena provides an ideal scenario for investigating these phenomena.

EDAPHIC DIFFERENCES, REGIONAL AND LOCAL

For two main reasons, the North Coast Biodiversity Arena is particularly valuable for analyzing adaptive plant evolution and speciation. First, the general position of the NCBDA relative to California's gradient climate is intermediate between that of deserts and steppes, and that of dense forests either tropical or temperate. In more arid climates, drier sites have such depauperate plant communities and extreme individual adaptations to aridity that opportunities for comparison of adaptations among the organisms are highly limited. Forests in more mesic climates are generally underlain by soils that have been so much modified by deposition and decay of organic matter that they reflect very poorly differences in parent material and geological history. Within most of the NCBDA, the intermediate climate tends to emphasize differences in soil type, texture, mineral content, and chemical content of parent materials which are often strongly manifest and influence greatly the varied success of competing species. Furthermore, microclimates based upon the rugged topography in combination with strongly manifest edaphic influences, often allow juxtaposition of plant associations and the survival of combinations of plant taxa unusual for central California.

Second, if we consider also the geological time scale and current knowledge and theories about the history of California's landscapes and its flora (Raven and Axelrod 1978; Schaffer 1993; Wilkin 1993), we must appreciate even more highly the value of the NCBDA. From the time when modern angiosperms occupied lands that were to become California, right up to the present, a succession of crustal movements, displacement of mountains, elevation of new mountain ranges, volcanism, and climatic changes, have occurred. These shifting climates and landscapes gave rise both to changes in plant species diversity and in the nature of the transitions between different ecological habitats evident throughout the NCBDA. Three situations are particularly worthy of mention: 1) the transition from grassland or chaparral to oak or mixed evergreen forest; 2) the unpredictable occurrences of species in marginal mixed conifer-redwood associations; and, 3) the often sharp boundary along the coast between mixed conifer-redwood and closed-cone pine forest.

As a background, the topography and geology of the area can be described as follows: On the eastern margin presently uptilted Cretaceous marine strata (120–70 MYBP), were deposited on the shores of the Sacramento Sea, which at that time occupied the present site of the Central Valley. These marine strata alternate between layers of sandstone, composed of coarse sands and gravels deposited during periods of active uplift; and shales, consolidated muds and clays laid down during periods of relative geological quiescence. Within the NCBDA these formations compose the Vaca Mountains, the ridge between Capay Valley and Lake Berryessa, and the low ranges to the north adjacent to the western margin of the Central Valley. The vegetation and flora occupying these parent materials are those typical of the inner North Coast Ranges and are developed as two major vegetation types: 1) woodlands and savannas dominated by *Quercus wislizenii* (interior live oak), and *Quercus douglasii* (blue oak); and, 2) chaparral composed mostly of *Adenostoma fasciculatum* (chamise) and *Quercus berberidifolia* (scrub oak).

The central and western sectors are underlain chiefly by metamorphic rocks of the Franciscan series, ranging in age from Jurassic to Cretaceous (150–100 MYBP). More recent formations outcrop near the eastern boundary of the central sector, and along the Pacific coast. As regards the former, during the Pliocene epoch (7–3 MYBP) volcanic eruptions partly covered the hills surrounding the Napa and Sonoma valleys of the central sector with lava, volcanic ash, and mudflow breccias. Subsequent tectonic uplift and faulting has created a patchwork of parent materials that now support an equally complex pattern of forest elements. This complex geologic and floristic patterning centers about Howell Mountain, particularly its steep northeast-facing slopes. An ecological analysis of the mixed evergreen forest found in this area should increase greatly our understanding of the mixed evergreen forest type as a whole, at least with reference to its Californian facie. Equally complex geologies and floristic patterns extend to the southwest as far as the Sonoma Valley, and northwest to Mt. St. Helena.

Turning to the western edge of the NCBDA, geologists have recognized its coastal formations from Fort Ross north to Stewarts Point as the northernmost extremity of faulting and movement along the San Andreas fault. West of the fault line itself, in the region of Fort Ross and Salt Point State Parks and the intervening area, coastal vegetation is completely different from that which flourishes less than a kilometer inland (~½ mile), e.g., at Kruse Rhododendron State Reserve. Preliminary evidence based upon soil chemical composition and soil depth suggests that analysis of this area within the NCBDA with reference to these factors, would be most rewarding and may provide clarification of the relative importance of chemical versus physical edaphic conditions as they influence vegetation and floristic patterns.

In the forests of the western sector, high soil and atmospheric moisture combined with relatively equable temperatures promote increased biomass and accumulation of surface litter. The resulting increase in organic content of surface soils promotes the spread of species that are unique to this area within the NCBDA, e.g., *Scoliopus bigelovii, Clintonia andrewsiana,* and *Hierochloë occidentalis.*

The Diversity of Edaphic Islands

In this discussion, edaphic islands are defined as restricted areas distinguished by a soil type or parent material markedly different from that of the surrounding region, supporting one or more highly localized species possibly endemic to the edaphic type. The present area contains three widespread and distinctive kinds of edaphic islands, each of which depends upon a different edaphic characteristic.

1. Serpentine islands. Serpentine islands are associated with the Franciscan formation (Jurassic–Cretaceous), and are scattered throughout the area. South of the NCBDA, in the San Francisco Bay Floristic Province (SnFrB), they occur chiefly in association with the San Andreas Fault. North of the San Francisco Bay, including the NCBDA and other areas to the north, particularly the Klamath–Siskiyou region, the serpentine occurs near areas of volcanic activity, and may have been emplaced at the land surface in association with newly forming volcanoes (E. Moores, personal communication).

Serpentine soils are derived by weathering from ferro-magnesium silicate (ultramafic) parent materials. Ultramafic rocks have a relatively high content of iron and magnesium and little or no calcium. Plant endemics that have become adapted to them differ greatly in composition and abundance among the serpentine islands depending on the degree of weathering, the chemical and physical attributes of the serpentinite, and available soil and atmospheric moisture. In general, serpentine islands found in the western sector are relatively small and widely separated, while those in the central and eastern sectors are larger, sometimes merging into each other. These size and distributional differences among the serpentine islands are reflected in the distribution of the endemic plant species. Many of the plants restricted to serpentinite in the western sector are highly restricted, and may be related to serpentine endemics found outside of the NCBDA, while those in the central and eastern sectors are usually more widespread within the NCBDA and have disjunct distributions in different serpentine islands. The most widespread serpentine specialists in and near the NCBDA are *Ceanothus jepsonii* (musk brush), *Cupressus sargentii* (Sargent cypress), *Quercus durata* (leather oak), and *C. macnabiana* (MacNab cypress). The latter pair of species occur also on other kinds of edaphic islands.

Since the NCBDA contains several evolutionary complexes that include a combination of serpentine endemics and closely related species or races that do not grow on serpentine e.g., the *Streptanthus glandulosus* complex (Mayer and Soltis 1994), the area offers unusual opportunities for experimental analysis of genetic characters, particularly those that might increase the fitness of genotypes adapting to this unusual habitat. Particular attention should be paid to *Ceanothus* subg. *Cerastes*, and *Hesperolinon* in addition to the *Streptanthus* complex mentioned above.

2. Hard rock volcanics. The central sector of the NCBDA is strongly influenced by the Pliocene volcanic activity centered near Howell Mountain. Volcanic activity is manifest in surface geologic formations extending in the south from near the cities of Napa and Sonoma, north to Mount St. Helena. Outpourings of lava and other molten rock hardened into geologic formations that erode very slowly, yielding a very thin soil that becomes saturated during the winter and dries out rapidly during the early spring. Sites with this shallow soil subject to saturation and rapid drying are often dominated by specialized endemics adapted to tolerate these environmentally stressful conditions. Along the east side of the Napa Valley, where the hard rock layers are only slightly tilted, the endemic *Ceanothus purpureus* forms large populations. Elsewhere, particularly along the unnamed ridge north of Mt. George that culminates in Atlas Peak, and along various parts of the Mt. Veeder–Hoods Peak Range to the west a distinctive annual endemic, *Madia nutans,* is adapted to this harsh habitat. Indirect evidence suggests a relatively recent origin for these narrow endemics, but this problem needs to be attacked using molecular techniques, particularly polymerase chain reaction-assisted DNA analyses.

3. Fossilized volcanic ash. Pliocene volcanic activity in the NCBDA distributed mineral ash layers over a wide area. Ash layers that did not become eroded away became embedded with older geologic strata as a result of faulting and uplift. Soils consisting largely of this mineral ash are acidic, low in major nutrients, and produce physiologic stresses unfavorable to the dominant species e.g., *Pseudotsuga menziesii, Arbutus menziesii*, and *Quercus kelloggii.* In these highly localized sites, the dominant forest taxa are replaced by stress tolerant species such as *Pinus attenuata* (Knobcone pine), *Arctostaphylos canescens* (hoary manzanita), *A. standfordiana* (Stanford's manzanita), *Xerophyllum tenax* (beargrass), *Salvia sonomensis* (Sonoma sage), and *Cupressus macnabiana.* The best example of a fossilized volcanic ash edaphic island is found along Cavedale Road, Sonoma County, and contains these alternate forest species which among other taxa have entered the edaphic island from various directions and divergent habitats. Representative species at Cavedale which are well-developed in other parts of the North Coast Biodiversity Arena include *Pinus attenuata*, *Arctostaphylos* spp. and *Salvia sonomensis.* Species from more xeric regions include *Cupressus macnabiana* and *Helianthus gracilentus* (slender sunflower). Those species with their best development on more mesic higher mountain slopes include *Xerophyllum tenax* and *Viola lobata* (pine violet). Taxa found mostly in the equable coastal zone to the west are represented at Cavedale by *Chrysolepis chrysophylla* var. *minor* (dwarf chinquapin) and *Solidago spathulata* (coast goldenrod). The disparity of these sources is clear evidence that the distribution and establishment of these invasive species is independent of surrounding species, and is governed chiefly by the availability of a niche to which they can become adapted.

THE VEGETATION OF THE TRANSECT

Description and characterization of the vegetation within the North Coast Biodiversity Arena is the most difficult section of this review. This is because the literature in ecology has for a century been cluttered with numerous attempts to define a few easily recognizable principles, trends, or categories, none of which has succeeded. This problem has been reviewed in a reasonably successful manner by Barbour et al. (1993), and in a different way by Begon et al. (1986). A further complication is that the recent floristic classification of the area by Hickman (1993) has added the names of floristic provinces and subprovinces that have previously been mentioned, and these must be considered in connection with any proposed classification.

We have already recognized that the NCBDA flora should be included in three floristic subprovinces, North Coast (NCo), North Coast Ranges Outer (NCoRO), and North Coast Ranges Inner (NCoRI). Although the division between the NCoRO and NCoRI is difficult to place physically within the NCBDA, a classification of the vegetation is even less clear-cut, primarily because of the large number of edaphic islands with their unique combinations of flora.

We follow Barbour et al. (1993, pp. 6–7) in recognizing a relatively small number of vegetation types. These are defined chiefly on the basis of climatic and edaphic factors that affect the association of species in a particular area. Thus, we recognize within the area seven vegetation types, as follows: 1) Coast Interface (sensu Barbour et al. 1993); 2) Mixed Evergreen Non-Riparian Forest; 3) Mixed Riparian Forest; 4) Single Tree-species Forests/Woodlands individually dominated by: A. *Pinus muricata* B. *Quercus wislizenii*, C. *Cupressus sargentii*, and D. *Pinus attenuata*; 5) Oak-savanna-grasslands; 6) Brushland Communities; and 7) Wetland Communities.

1. Coast interface. Edaphic diversity permits recognition of three separate subdivisions: 1) sandy beach and dunes; 2) rocky shore and coastal bluff; 3) coastal scrub and grassland, dominated by *Baccharis pilularis* (coyote brush), both upright and prostrate forms plus intermediates. The subdivisions of this type are united through their direct exposure to winter storms and summer fogs, linear shape several kilometers in length from north to south, and width from shore to inland mixed forest varying from only a few tens of meters to at most one or two kilometers. Although the great majority of the species included are either widespread along the Pacific Coast or are found chiefly south of the area e.g., *Dudleya farinosa* (rock lettuce), a few are more northern in distribution, e.g., *Polypodium scouleri* (Scouler's polypody). Northward in Mendocino County, the subdivisions assume a more northern aspect, particularly with respect to the conifers that separate the redwood and mixed evergreen forests from the coast itself. There *Picea sitchensis* (Sitka spruce) and *Pinus contorta* (shore pine) may locally replace *Pinus muricata.*

Except for *Baccharis,* the species that make up this vegetation exhibit little relationship to those of the interior vegetational types of the NCBDA, and so are not discussed. On the other hand, *Baccharis pilularis* requires special attention, since it illustrates the principle of edaphic compensation. The upright form of *Baccharis pilularis* is the most common species in the NCBDA that clearly illustrates this principle. At the extreme of the western sector, exposed to the cool foggy climate of the immediate coast, *Baccharis* succeeds best on the warmest driest slopes where soil water retention is low. In Cold Canyon near Monticello Dam at Lake Berryessa in the eastern sector at the opposite edge of the NCBDA, *Baccharis* is a subriparian species that can resist the stress of drought and heat only by growing as near to the stream bed as possible. This principle may be applicable to a large proportion of those species distributed over the entire NCBDA.

The phenomenon of edaphic compensation in *Baccharis* highlights a basic problem of evolutionary genetics in plants. Is compensation achieved by phenotypic modification of one or a few similar genotypes, or is it achieved by mutation, recombination and natural selection involving many genes and gene systems, and accompanied by major processes of directional Darwinian selection? If the latter is true, what is the nature of the gene systems involved, in terms of the developmental-physiological action of their products?

Representing an initial approach to a solution of this problem are the experiments of (Clausen et al. 1940; Clausen and Hiesey 1958). On the basis of their results one can conclude that approximately one-half of the phenotypic differences between *Potentilla glandulosa* from timberline and foothill ecotypes in the Sierra Nevada is based on genetic differences and the other half on phenotypic modification.

A related experiment on *Rhododendron occidentale* (western azalea) backed by molecular data on electrophoretically active enzymes, has shown NCBDA western sector populations differing from eastern sector populations not only with respect to factors probably associated with climatic differences, but also with respect to the abundance and distribution of trichomes that may serve as insect repellents. Moreover, some of the azalea populations, particularly those located in the eastern sector, grow preferentially on serpentine soil, and have developed adaptations to the stresses that it imposes (Hrusa, ms. in prep.).

2. *Mixed evergreen forest.* Between one-third and one-half of the NCBDA is covered with a forest consisting of conifers, broad-leaved evergreens and broad-leaved deciduous trees, chiefly oak species. Authors have attempted to divide the mixed evergreen forest into communities or sets of communities (Holland 1986; Sawyer et al. 1988), but according to our observations these components blend into each other, except where separated by distance. As clearly recognized by Barbour et al. (1993), the mixed evergreen forest of northwestern California is only a southward extension of the vast holarctic coniferous forest that encircles the northern hemisphere between latitudes 45° and 55° north. Except in coastal California and a few other places, it is dominated in the United States by three widespread species; *Pseudotsuga menziesii*, *Pinus ponderosa*, and *Picea engelmannii* (Engelmann spruce). In Canada it is dominated by species of *Abies* and *Picea*.

There is no doubt that the California version of this forest, on the whole, contains dominant trees that exhibit a range of physiological optima. In rough order of preference for mesic conditions are *Sequoia sempervirens* (coast redwood), *Pseudotsuga menziesii*, then *Lithocarpus densiflora* (tanoak), followed by madrone *Arbutus menziesii* and the subdominants *Quercus garryana* (Oregon oak), *Umbellularia californica* (California bay) and *Quercus kelloggii*. Nevertheless, unless careful comparisons of undershrubs and perennial herbs give support to any classification that might be suggested, we doubt that a subdivision into distinct communities can be realistically maintained. Impressive and distinctive as it appears to be at first sight, we believe that the *Sequoia sempervirens* forest can be recognized only informally as a region of the larger forest area. This opinion is based upon comparisons of forests containing redwood which are found within the NCBDA from near the immediate coastline to the eastern sector's western boundary. These latter redwood groves are the most interior localities known for the species and occur outside regular summer fog cover nearly 60 kilometers from the coast.

Based upon observations in Humboldt County, Barbour et al. (1993) describe a series of climax distributions based on altitude. In our area, however, similar distributions occur in a serial fashion at altitudes less than 450 meters (1500 feet). Therefore the distributions are probably attributable to differences in fog persistence affecting summer temperatures, as well as proximity to streams, microclimatic factors such as slope orientation and specialized edaphic conditions.

3. Riparian mixed forest. Since the NCBDA was purposely delimited to avoid the coastal valleys and rivers, it does not include any highly developed riparian forests. The only river that flows through the NCBDA for any distance is the Russian River in the western sector. So far as we know, its riparian forest has not been investigated in detail. In the central sector, the Napa River flows past vineyards for most of its length and has little undisturbed riparian forest, except for a remnant near Yountville managed as a reserve by the California Department of Fish & Game. In the eastern sector lies the drainage of Putah Creek, much of which has been converted by the Monticello Dam into Lake Berryessa. Hence, as compared to other parts of Northern California, the present area is unfavorable for investigating major riparian forests and the species they contain.

Nevertheless, the NCBDA contains a large number of lower order streams, bordered by distinctive species. Several of these are the only species of their genus found in the area, such as *Calycanthus occidentalis* (spicebush), *Cercis occidentalis* (western redbud), *Acer macrophyllum* (big-leaf maple), *Amelanchier alnifolia* (sarvis), *Aralia californica* (elk clover) and *Vitis californica* (wild grape). Because most of these species occur in at least two and often all three sectors of the NCBDA, and except for *Calycanthus, Cercis,* and *Amelanchier* belong to genera that have numerous species in other parts of their geographic ranges where they are not strictly riparian, the local evidence supports the possibility that the local mesic riparian environment is not conducive to speciation. This hypothesis is supported by the numbers of species exist, both generally and in the NCBDA, in the two genera of Salicaceae, the most characteristically riparian of northern temperate genera. The genus *Populus,* which is predominantly riparian, contains only about 40 species, while *Salix,* in which several riparian species are accompanied by a larger number that are adapted to meadows, bogs, wet mountainsides and other non-riparian habitats, contains approximately 400 species. The genus *Salix* is well-recognized for its many difficult taxonomic and evolutionary problems, including polyploidy and in the NCBDA, adaptation to serpentine.

Several year-round streams cut through serpentine rock, such as Austin Creek (western sector), Little Stony Creek and Butts Creek (both eastern sector). These serpentine riparian sites support a distinctive flora with many relictual endemics e.g., *Senecio clevelandii* (Cleveland's ragwort) and *Delphinium uliginosum* (bog larkspur), in addition to species disjunct from other regions e.g., *Castilleja miniata* (great red paintbrush) and *Parnassia californica* (grass-of-Parnassus).

4. Single tree-species forests/woodlands. In addition to the complex mixed evergreen forest, the NCBDA includes part or all of four forest types that are each dominated by a different single tree-species. These single tree-species forests/woodlands are each associated with a particular stressful habitat, and may be restricted to a specialized edaphic type.

A. Bishop pine (Pinus muricata) forest. At the western margin of the NCBDA, on coastal terraces from Fort Ross and Salt Point northward to beyond our area in northern Mendocino County, occurs *Pinus muricata*, a closed-cone pine of southern affinities. In our area the flora associated with *P. muricata* is particularly depauperate. This is due in part to the exposure of the coast to severe winter storms that twist many trees into fantastic shapes beloved by artists (Smith and Wheeler 1990–1991). A suspected but undocumented second factor is shallow soil. In this regard coastal terraces are known for their poorly drained highly podzolized soils on which pygmy forests including bishop pine sometimes occur (Baker 1972) and thus, relatively shallow and impermeable subsoil may contribute to the presence of bishop pine forest in our area.

B. Knobcone pine (Pinus attenuata) forest. Closely related to the bishop pine, knobcone pine forms nearly pure forests on the ridge between Hood Mountain and Mount Veeder (see Fig. 1). The pines occur in various-sized stands interpolated within the dominant mixed evergreen forest. These stands of *Pinus attenuata* are restricted to the fossilized volcanic ash deposits described previously. Associated plant species range from the diverse flora of mesic and north-facing slopes as described for the Cavedale Road edaphic island to understories restricted to *Arctostaphylos stanfordiana, A. canescens* and *A. glandulosa* on dry south to west-facing slopes. In the northern portions of its range *Pinus attenuata* occurs mostly on serpentine (Kruckeberg 1984) and indeed it is found on serpentine in the NCBDA in the northern central sector near the summit of Red Mountain South between Hopland and Ukiah (Smith and Wheeler 1990–1991). *Pinus attenuata* is also found on peaks and higher north-facing slopes in northern Lake County (McCarten 1988), but these and the Mendocino County occurrences on serpentine all appear to exceed the 500 meter elevation limit for the NCBDA. The best developed stands in the NCBDA at elevations below 500 meters occur on volcanic ash in the southern region, where knobcone pine is so tightly adapted to the ash deposits that on sites where ash and serpentine interfinger such as near Aetna Springs above Pope Valley, *Pinus attenuata* avoids the serpentine and occurs only on volcanic ash. The genetic basis for this differential adaptation to serpentine and volcanic ash should be investigated because within the NCBDA these substrata support generally exclusive floras. Among the remaining woody species of the NCBDA *Quercus durata* and *Umbellularia* also occur on both ash and serpentine. *Quercus durata* attains its best development on serpentine and where it grows on volcanic ash its form tends to vary slightly toward *Q. berberidifolia* which within the NCBDA is found only on unspecialized substrata. The biology of *Umbellularia* is poorly known and essentially nothing can be said regarding the edaphic factors involved in its distribution. Preliminary investigation of morphological variation in *Umbellularia* across edaphic and climatic variables suggests that while racial variation probably does exist, the patterns are complex and in need of further clarification.

C. Sargent cypress (Cupressus sargentii) forest. The final single tree-species forest to deserve attention is *Cupressus sargentii* which occurs in several large stands on hillsides underlain by serpentine soil. This single tree-species forest deserves attention in the NCBDA because the growth habit of the cypresses may approach that of *Cupressus macnabiana,* although the trees generally have the differentiating characters of *Cupressus sargentii.* Distinguishing *Cupressus sargentii* and *C. macnabiana* in the NCBDA is often highly subjective and an investigation of the patterns of variation among the NCBDA populations of these two cypresses would do much to clarify their overall relationship. A little known stand on the west side of Lake Berryessa is dominated by dwarf trees usually less than 2 meters in height. When explored carefully, this forest may be found to contain serpentine endemic races or species that are as yet unrecognized.

D. Interior live oak (Quercus wislizenii) woodland. In the eastern sector at the margin of the NCBDA, the slopes of the Vaca Mountains facing the Central Valley contain in protected canyon bottoms and on northeast-facing slopes a forest consisting almost entirely of *Quercus wislizenii* with scattered individuals of *Aesculus californica* (California buckeye). In the more mesic enclaves of this single tree-species woodland the herbaceous flora contains species found throughout the NCBDA, e.g., *Cardamine californica* (milkmaids), *Fritillaria affine* (checker lily), and *Dodecatheon hendersonii* (shooting stars). Drier sites support species of limited distribution within the NCBDA but which extend in range to the Sierra Nevada foothills, e.g., *Chorizanthe membranacea* (pink spineflower), or are disjunct from regions to the south, e.g., *Gutierrezia californica* (snakeweed).

5. Oak savanna-grasslands. The grassland savanna vegetation type within the NCBDA has been so much disturbed during the past 200 years by livestock grazing and introduction of European annuals that evolutionary investigations based on this type will not be sufficiently rewarding to justify the time and money necessary for them.

6. Brushland associations. Investigations of shrubland or chaparral will be most rewarding. Two genera that include the majority of woody species found in this vegetation type deserve particular attention, *Arctostaphylos* and *Ceanothus.* Of these two, *Arctostaphylos,* although well represented in the NCBDA, is richer in endemic species from the San Francisco Bay Province southward into Baja California. Moreover, it has proved to be difficult in the way of genetic investigations. Although seed germination under artificial conditions has been successful for most species, percentages are too low to enable unbiased progenies to be raised from either artificial or suspected interspecific hybrids or their parents. Although generation by generation analyses of allozyme alleles will partly overcome this defect, it is doubtful that it can be fully overcome.

On the other hand, species and hybrids of *Ceanothus* are routinely grown from seeds in gardens and arboreta (Schopmeyer 1974). Of the two subgenera of *Ceanothus, Euceanothus* and *Cerastes,* there are respectively seven and twelve taxa found within the NCBDA. A center of recent speciation in *Cerastes* is in or near the NCBDA, as evidenced by the six narrowly endemic taxa of the total of twelve found there (Schmidt 1993). In contrast there are no endemics among the six species of *Euceanothus* within the NCBDA. Over the range of the entire genus *Ceanothus,* the ratio of narrow endemics to widespread taxa is considerably broader in subgenus *Euceanothus* than in subgenus *Cerastes.* An interesting problem of phytogeography and evolutionary ecology is why this pattern should occur within a single genus.

At the opposite extreme is the most common dominant species of chaparral, *Adenostoma fasciculatum*, which has no living relatives except for its localized congener *A. sparsifolium* (redshanks) of desert margin habitats. Axelrod (personal communication) believes that *Adenostoma* must have originated no more recently than 9–10 million years ago in the Upper Miocene, and in spite of an increase and fluctuations during the subsequent millennia of habitats favorable to it, has not given rise to any derivative taxa, or at least none that are extant. Among the three sectors of the NCBDA *Adenostoma* is found in each on a diversity of substrata and in various exposures. The species is genetically distinctive among habitats in central California (Anderson 1954). Within the NCBDA its pattern of variation across habitats is unknown.

7. Wetland associations. Wetland habitats are among the most impacted in California; probably only the annual grasslands are more altered from their pristine state. Throughout the NCBDA there occur many small and large springs, at least one major wetland—Pitkin Marsh—in the western sector, and a remnant set of vernal pools in the vicinity of Santa Rosa, all of which have been severely impacted. There are numerous hot springs concentrated in the volcanic region immediately south of Mt. St. Helena, but most of these have been converted to resort use. Immediately northwest of Mt. St. Helena occur the endemic taxa *Poa napensis* (Napa bluegrass), and *Dichanthelium lanuginosum* var. *thermale* sensu Spellenberg (Geysers dichanthelium), both of which are restricted to warm, moist, alkaline sites near The Geysers in the Mayacmas Mountains. The wetland habitats within the NCBDA are so altered we feel they are no longer of broad value for evolutionary studies. Ecological questions may be addressed in specific localities, but overall the habitat is relatively unproductive in terms of evolutionary studies at the present time.

ECOLOGICAL STABILITY, CHANGE AND SPECIATION

Previous experience with higher plants, plus observations during the present season within the NCBDA have strengthened our belief that speciation rates measured in terms of established species depend as much or more upon the diversity of the habitat as it affects Darwinian natural selection, than upon genetic processes occurring within individuals and populations. The present section of this review starts with the assumption that this hypothesis is correct, and asks the question: Are the resources of genetic and specific variation among the genera found within the NCBDA great enough, and of such a nature that investigations of its plant populations will lead to a testing of this hypothesis and to a greater understanding of speciation in general?

A review of the genera found within the area shows that among them are at least 22 that present interesting problems. These concern six degrees of divergence. Some levels of divergence remain strictly at the racial level e.g., *Rhododendron occidentale* and *Umbellularia* as discussed previously. The next two defined levels of divergence have biologically imperfectly isolated species-pairs occurring with or without some degree of fidelity to specialized climatic or edaphic situations. The first group includes among others the recognizable species-pairs, *Rhamus californica/tomentella, Monardella viridis/villosa,* and *Delphinium decorum/nudicaule.* The latter pair of species are especially interesting due to their divergent floral forms based upon developmental paedomorphy. In this light the evolution of the narrow endemic *Delphinium luteum* by hybridization of *D. decorum* and *D. nudicaule* (Guerrant 1978) is of special interest. The second group has species that can usually be recognized in nature but among which isolating barriers of a genetic nature are weak or absent e.g., *Rhamnus crocea/ilicifolia* which intergrade across a climatic gradient, *Ceanothus* subg. *Cerastes* discussed in detail in a previous section and whose species tend to display edaphic fidelity, and the genus *Quercus* which across the NCBDA has numerous interesting problems concerning hybridization and introgression. Then come genera within which species are strongly isolated from each other based upon genetic-developmental barriers that affect growth as in *Linanthus* (*L. bicolor*/cf. *androsaceus*) where different somatic DNA content and differential sensitivity to artificially applied growth substances reflect differences in the natural environment of the species (Stebbins, unpublished data). Finally there are examples of genera that contain strongly isolated subgenera, within each of which isolating barriers are of a different nature (*Madia nutans/rammii* vs. *Madia stebbinsii/hallii*), and at the strictly macroevolutionary level are genera of which the taxonomic position is doubtful (*Calycanthus, Umbellularia*) and whose affinities may be revealed by molecular methods.

These examples and others will be discussed in greater detail elsewhere. Here, only two more general points need to be emphasized, although their solutions would benefit by investigation within the NCBDA. First, the preliminary data show that several different patterns of speciation exist, and that their occurrence is independent of the taxonomic position of the entities involved. Three examples show striking differences between closely related genera or subgenera. First, in the Ericaceae, *Arbutus* in California consists of a single homogeneous species that, according to fossil evidence, may be at least 25–30 million years old. The neighboring genus *Arctostaphylos* is certainly no older, but is divisible into an indefinite number of species, ranging 50–80, depending upon taxonomic treatment.

Second, in the Fagaceae, *Lithocarpus densiflora* is a single species that on the basis of fossil evidence including both leaves and acorn cups is at least 40 million years old, while *Quercus* species that either migrated into California or originated there during the past 25–30 million years appear to have given rise to several additional species during the past ten million years.

In the Fabaceae, *Pickeringia* (chaparral pea) and *Thermopsis* (false lupine) both contain only a single species in California, where they are frequent to common members of chaparral (*Pickeringia*) or woodland communities (*Thermopsis*) across the NCBDA. In contrast, the very similar genus *Lupinus* contains a total of 60–70 species in California, dominated by perennials, a number of which are in the NCBDA. *Pickeringia* and *Thermopsis* are somewhat isolated within the Fabaceae, based on the state of their stamen filaments, that are free and separate, whereas in nearly all other California genera of the family, including *Lupinus,* nine of the ten filaments are fused. These three genera resemble each other in most other characters and often grow in similar habitats. Can it be that the mere difference between free vs. fused stamen filaments can be the cause of this great difference in speciation? The development, floral biology and pollination biology of these three genera is well worth investigating.

The present review has shown that recognition of the North Coast Biodiversity Arena has not solved any problems associated with diversity of speciation or with phylogeny. Nevertheless it has been the source of research guidelines and of groups of species highly suitable for this purpose. These guidelines can be applied equally well to the more challenging problems posed by tropical floras. To those young men and women who have become "hooked" on the idea of using observations on natural history to solve problems of plant evolution, we can give you a relevant quotation, but we can't give you its source. The senior author learned it 80 years ago, when playing with Richter's Anchor Blocks:

> "We play at paste 'til qualified for pearl
> then throw the paste aside and think ourselves deceived
> the shapes, though, are similar and our rough hands carve
> diamonds while playing with sand."

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Appendix I. Established Public and Private Reserves, Parks and Forests Within the North Coast Biodiversity Arena. This compendium is not exhaustive; it is intended to emphasize the large number of potential sites available to those planning research or educational excursions within the NCBDA. Those interested in visiting any of these sites to ascertain their suitability for projects or class visits should contact the organization or agency listed. There are in addition large tracts of land within the NCBDA administered by the United States Forest Service. National Forest land is most extensive in the area north of Clear Lake. Sites are grouped alphabetically within sector and the major points of botanical interest at each site are listed. Abbreviations: *Land administrators:* California Department of Parks and Recreation (CDPR), Napa Land Trust, Napa California (NLT), California Department of Fish & Game (CDFG), California Department of Forestry (CDF), California Academy of Sciences (CAS), United States Forest Service (USFS), The Nature Conservancy (TNC), University of California Natural Reserve System (UC). *Botanical or Geologic Specialty: Botanical Specialty:* Coast interface (CI), mixed evergreen (ME), mixed evergreen with *Sequoia* (ME-*Sequoia*), riparian (R), riparian with *Sequoia* dominant (R-*Sequoia*), chaparral (C), single tree-species forest/bishop pine (STF/Bishop Pine), single tree-species forest/*Cupressus* (STF/*Cupressus*), single tree-species forest/*Quercus wislizenii* (STF/*Quercus*), oak woodlands-various species mixtures (OW), oak woodlands/savanna (OW/S). *Geologic Specialty:* Serpentine (SERP), hard rock volcanics (VOL), fossilized volcanic ash (ASH).

Site name	Administrator	Bot/Geo specialty
	Western sector	
Armstrong Redwoods State Reserve	CDPR	*Sequoia,* R
Austin Creek State Recreation Area	CDPR	SERP, ME-Sequoia, C, R, OW
Fort Ross State Historical Park	CDPR	STF/Bishop Pine

APPENDIX I. CONTINUED

Site name	Administrator	Bot/Geo specialty
Harrison Grade Ecological Reserve	CDFG	SERP, STF/*Cupressus*
Kruse Rhododendron State Reserve	CDPR	ME-*Sequoia*
Laguna de Santa Rosa Ecological Reserve	CDFG	R
Salt Point State Park	CDPR	STF/BP, CI
Sonoma State Beaches	CDPR	CI
Stillwater Cove County Park	County of Sonoma	CI
Yorkville Ecological Reserve	CDFG	SERP
	Central Sector	
Annadel State Park	CDPR	ME-*Sequoia*
Archer Taylor Reserve	NLT	ME-*Sequoia,* C, ASH
Bothe-NAPA Valley State Park	CDPR	ME-*Sequoia*
Bouverie Reserve	NLT	ME, VOL
Fairfield Osborne Reserve	TNC	wetland, vernal pool, R, OW, ME
Hood Mountain Regional Park	County of Sonoma	ME
Lake Hennessey Rec. Area	City of Napa	OW, SERP
Las Posadas State Forest	CDF	ME, R-*Sequoia*
Mount George Reserve	NLT	C, VOL
NAPA River Eco. Reserve	CDFG	R
NAPA River State Park	CDPR	R
Pepperwood Reserve	CAS	OW, ME, SERP
Robert Louis Stevenson State Park	CDPR	ME, C
Sonoma Valley Regional Park	County of Sonoma	OW, ME
Sugarloaf Ridge State Park	CDPR	ME, R-*Sequoia,* C, OW/S, SERP, VOL
	Eastern Sector	
Frenzel Creek Research Natural Area	USFS	STF/*Cupressus,* R, SERP
Lake Berryessa State Recreation Area	CDPR	OW, C, STF/*Cupressus,* SERP
Quail Ridge Reserve	UC	OW, C
Stebbins Cold Canyon Reserve	UC	STF/*Quercus*, OW/S, C, R
Wantraub Reserve, Pope Valley	NLT	OW/S

APPENDIX II. PUBLIC AND PRIVATE FOUR YEAR UNIVERSITIES WITHIN A CONVENIENT DISTANCE OF THE NORTH COAST BIODIVERSITY ARENA.

University or college	Location	County
California State University	Chico	Butte
California State University	Hayward	Alameda
California State University	Humboldt	Humboldt
California State University	Sacramento	Sacramento
California State University	Sonoma	Sonoma
California State University	Stanislaus	Stanislaus
Mills College	Oakland	Alameda
Pacific Union College	Angwin	Napa
San Francisco State University		San Francisco
San Jose State University		Santa Clara
Stanford University	Stanford	San Mateo
University of California	Berkeley	Alameda
University of California	Davis	Yolo
University of California	Santa Cruz	Santa Cruz
University of the Pacific	Stockton	San Joaquin